Fig. 6. Lateral view of terminal structures of larval Trichopteron.

Fig. 7. Frontal view of pupal head of *Philopotamus* only mandibles shown.

Fig. 8. Dorsal view of thorax and wing bases of *Mnemonica auricyanea*, Wals.

Fig. 9. Frontal view of pupal head of *Mnemonica auricyanea*, Wals.

A COMPARISON OF THE GENITALIA OF MALE HYMENOPTERA, MECOPTERA, NEUROPTERA, DIPTERA, TRICHOPTERA, LEPIDOPTERA, HOMOPTERA, AND STREPSIPTERA, WITH THOSE OF LOWER INSECTS.

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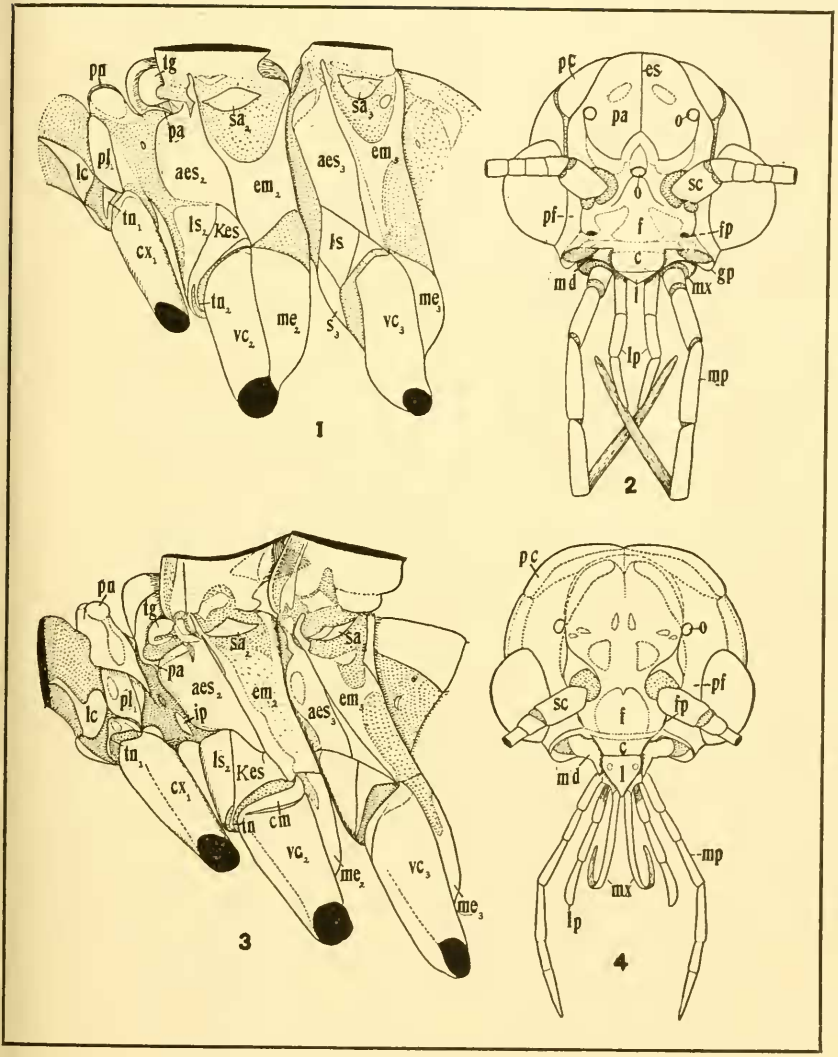
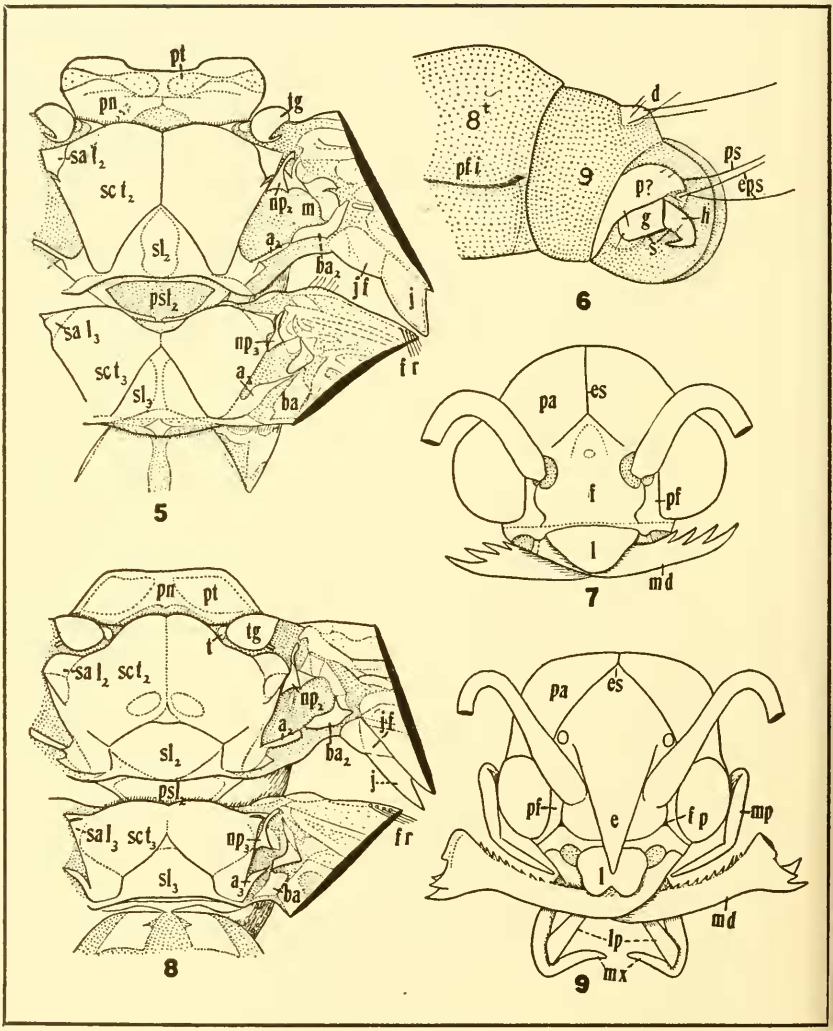
Since the same plates have been used to illustrate both the present paper, and the preceding one dealing with a comparison of the lower Lepidoptera with the Trichoptera, the same list of abbreviations will serve for both papers, and by referring to the explanation of the labeling, given on page 32, this will obviate the necessity of repeating in the present paper, the list of abbreviations there given. For the Strepsipteron here described, I am indebted to Dr. C. T. Brues. Dr. Bethune-Baker has loaned me the lepidopterous material used; Dr. R. J. Tillyard has furnished the neuropterous material; and Mr. S. A. Rohwer has furnished the sawfly material used in the preparation of this paper. Mr. Nathan Banks has very kindly identified the Trichopteron referred to, and Mr. A. N. Caudell has had the Homoptera identified for me. To all of these gentlemen, I would express my deep appreciation of their generosity and assistance so freely given.

The genitalia of male insects have been discussed in several recent articles; but the correct interpretation has not been given to the parts in all cases. Recently, however, I have been able to examine a far wider and more inclusive range of forms than was at first available for study, and the added evidence, together with that furnished in Dr. Walker's excellent account of the parts of the



CRAMPTON—Lower Lepidoptera and Trichoptera.



CRAMPTON—Lower Lepidoptera and Trichoptera.

male of the interesting insect *Grylloblatta campodeiformis*, has made it possible to revise the interpretation of the parts in the higher forms, in the light of the increased knowledge of the subject, gained from these sources.

For the purpose of the present paper, it is sufficient to begin the study of the modifications met with in the higher forms with a consideration of the condition exhibited by the primitive mayfly *Blasturus cupidus* (Fig. 11). The sternite of the ninth abdominal segment in this insect (labeled "ha" in Fig. 11, Plate IV) bears a pair of somewhat closely united, plate-like sclerites, called the styligers or "coxites," one of which is seen in profile in Fig. 11, where it bears the label "p." Dr. Walker correctly compares these styligers or "coxites" with the basal segments of abdominal limbs (protopodites ?) retained in such lower insects as *Machilis*, in which the styligers or "coxites" bear styli which are possibly homologous with the exopodites (or epipodites ?) of crustacean limbs. Similarly, in *Blasturus*, the styligers or "coxites" labeled "p" in Fig. 11, bear styli "s"; but in the latter insect, there are traces of two segments in the styli (and in some mayflies there are three or more segments in the styli), while the styli of most apterygotan insects are composed of but one segment. The segmented styli of ephemerids ("s" of Fig. 11) are called gonopods, gonostyli, or arthrostyli. Following Morgan, 1913, Eaton (Monograph of the Ephemerida), Berlese, 1909, and others who have figured the parts of male ephemerids, I formerly interpreted the plates "p" of Fig. 11 as representing the sternite of the tenth segment; but they are apparently structures belonging to the ninth segment, as pointed out above. In this connection, it should be noted that the designation "tenth segment" refers to the tenth *abdominal* segment, not including the three thoracic segments in the count, as is usually done by lepidopterists. Furthermore, it should be borne in mind that the actual first abdomnial sternite has become atrophied in most insects, and the first apparent sternite really represents the sternite of the second abdominal segment, so that it is preferable to count the segments on the dorsal side, where most of them are preserved in the lower forms.

Palmen, 1884 (page 42) in describing the development of the vasa deferentia of mayflies, states that they extend to the posterior

margin of the ninth sternite where they are inserted in the hypodermis. On page 47, he states that the penes (here homologized with the penis valves "pv") arise as two protuberances of the hypodermis in the location of the insertion of the vasa deferentia (*i. e.* on the posterior margin of the ninth sternite), so that the partially united appendages (labeled "pv" in Fig. 11) lying above and between the gonopods "s," and forming the phallus or penis of the male *Blasturus* may represent appendages of the ninth segment in addition to the gonopods "s." If both penes and gonopods are structures belonging to the ninth segment in such primitive forms as the mayflies, this fact is of considerable importance in attempting to determine to what segment structures homologous with them in the higher forms may be assigned; and this also has some bearing on the view that the penis valves "pv" represent the endopodites of a pair of abdominal limbs whose exopodites are formed by the gonopods "s," since in order to fulfil the latter conditions, both penis valves and gonopods would have to belong to the same segment—for it is clearly impossible for the exopodites of a pair of limbs to belong to one segment while the endopodites of the same limb belong to another segment. On the other hand, Wheeler, 1893 (p. 124) states that "the male ducts of *Blatta* end at first in terminal ampullæ enclosed by the appendages of the tenth abdominal segment just as in *Xiphidium*" but later "the terminal ampullæ lie completely in the ninth segment, having shifted their position headward" (p. 118). On page 132 he states that in *Xiphidium* and *Blatta* the male ampullæ lie "at the hind end of the ninth abdominal segment. Just as the deferent ducts of ephemerids extend to the penes and open to the exterior, so the terminal ampullæ originally extend into a pair of appendages, albeit on the tenth segment and not opening to the exterior. If the penes of the ephemerids are really modified ambulatory appendages they would be homologous with the styli of Orthoptera. The curious persistence of these appendages in existing Orthoptera may be due to their having once functioned as penes, long after the other abdominal ambulatory appendages have disappeared." While I would not agree with Wheeler in his suggestion that the penes of the ephemerids (which are apparently homologous with those of the blattids) represent the styli of the Orthoptera (*i. e.* that "pv" of Fig. 11 represent

"s" of Fig. 12), there is some reason to suppose that styliform appendages borne on the tenth abdominal segment of certain Trichopteron larvæ (see Plate III, fig. 6, "s") may take part in the formation of portions of the genitalia of the adult male, although this matter is greatly in need of further investigation.

The tenth tergite labeled "ep" in Fig. 11, overlaps the paraprocts "pr" which are situated on either side of the anal opening, and bear the cerci "ca." The paraprocts "pr" are latero-ventral structures of the eleventh segment, and are usually interpreted as representing the divided sternite of this segment, although it is quite possible that they represent the protopodite of the uropod whose endopodite forms the cercus. The eleventh tergite of the ephemerid shown in Fig. 11 bears a terminal filament or telofilum "tf." The eleventh tergite is usually atrophied in the higher forms, while the paraprocts "pr" usually unite with the tenth tergite "ep" to form a structure through which the anus opens (*i. e.* the "proctiger" of higher insects).

In the blattids (whose parts are of the type serving as the "starting point" for the modifications developing in the various orthopteroid insects) the styli-bearing plates "p" of Fig. 12, are usually indistinguishably united with the ninth sternite "ha," although in the roach shown in Fig. 12, traces of these plates are still retained. The styli, "s," however, usually remain distinct even after the plates bearing them have become indistinguishable fused with the ninth sternite. The penis valves "pv" of Fig. 12, possibly represent the paired organ "pv" of the ephemerid shown in Fig. 11, although the parts are asymmetrically developed in the roach. The tenth tergite "ep" is distinct in most blattids, as is also true of the paraprocts "pr" (Fig. 12); but the eleventh tergite is atrophied in these insects and their immediate relatives.

A different path of specialization is apparently followed in the higher insects although the condition occurring in these forms is probably a modification of the basic plan exhibited by the Ephemerida (Fig. 11). Thus in the Prohymenopteron (sawfly) shown in Fig. 17, the tergite of the ninth segment "9^t" becomes very small, while the sternite of the ninth segment is very large, and projects beneath the genitalia of the male to form the so-called hypandrium "ha." The tenth tergite "ep" is very small, and the paraprocts "pr" of Fig. 11, which bear the cerci "ca," have united with the

tenth tergite "ep" in the sawfly shown in Fig.17. In most sawflies, the ninth tergite "9^t" is greatly reduced, and the tenth tergite "ep" (Fig. 17) unites with it. In the siricid shown in Fig. 17, the basal sclerite "p" (interpreted as the tenth sternite by some entomologists) may possibly represent the plate labeled "p" in Fig. 11 of the ephemerid—though it is also possible (but not as probable) that the segment "g" of the genital claspers of the siricid shown in Fig. 17 represent the styligers "p" of the ephemerid (Fig. 11). In either case, the styliger region "p" of the sawfly (Fig. 17) would be distinct from the ninth sternite "ha" thus approximating the condition exhibited by *Grylloblatta campodeiformis*, which Walker considers unique in having styligers distinct from the ninth sternite. The two-segmented clasping forceps "s" composed of the segments labeled "g" and "h" in the sawfly shown in Fig. 17, may represent the claspers labeled "s" (and also composed of two segments labeled "g" and "h"—which however may not be the exact homologues of the segments bearing these labels in Fig. 17) in Fig. 11 of the ephemerid.[1] The penis valves "pv" composing the penis or phallus in the sawfly shown in Fig. 17, doubtless represent the penis valves "pv" of the ephemerid shown in Fig. 11. The sawfly group, or Prophymenoptera, is thus seen to have retained the primitive condition of the parts as nearly as any of the higher forms have done, and a study of the parts in the sawflies is therefore of considerable importance.

In the Mecopteron shown in Fig. 19, the tergite labeled "ep" doubtless represents the tergum of the ninth segment, while the tenth tergite has either united with it, or has become greatly reduced. The ninth sternite "ha" is well developed, and the gonopods are composed of two segments "g" and "h" which are possibly homologous with those bearing the same labels in Fig. 17. The sclerite labeled "p" in Fig. 17 apparently unites with the pleural region of the ninth segment in the Mecoptera (Fig. 19); and in the insect shown in Fig. 19, the penis valves, which are usually separate in the lower forms, have probably united to form the single membranous structure "pv." In the Mecopteron shown in Fig. 21, the plate "pp" represents the ventral and lateral portions of the ninth segment, while the ninth tergite becomes prolonged into two lobe-like processes labeled "sg," which are

[1] The parameres of Dermaptera and Coleoptera are also homologous with these structures.

extremely elongate in some *Bittacus*-like Mecoptera, and doubtless serve as clasping organs in mating. The basal segment "g" of the gonopods is very large in the Mecopteron shown in Fig. 21, while the terminal segment "h" is greatly reduced. The penis valves "pv," however, are quite large, are partially united, and bear a coiled penisfilum "b." The structure labeled "ep" probably represents the tenth tergite with which the paraprocts bearing the cerci "ca" have united. The structures labeled "ca" may not represent the cerci; but they occupy the position characteristic of these organs, and have been provisionally interpreted as the cerci in the present paper.

In the Strepsipteron shown in Fig. 18, the structure labeled "ep" is a "proctiger," since the anus opens at its posterior end. It is probably formed largely by the tenth tergite, although a portion of the ninth tergite may also be involved in its composition. The structure labeled "g" may represent the hypandrium or plate below the genitalia of the male (*i. e.* the ninth sternite) but I am inclined to think that the basal segment of the gonopods also enters into the composition of this structure, while the small hooks labeled "h" might possibly represent the terminal segments of the gonopods. The structure labeled "pv" is the ædeagus or phallus, and in some Strepsiptera an intromittent organ is protruded from the ædeagus at the time of mating.

The sternite of the ninth segment labeled "ha" in the Neuropteron shown in Fig. 20 is well developed and is demarked from the pleural region of the segment "pp." The ninth tergite is partially produced on either side to form a pair of lobe-like structures "sg," comparable to the copulatory lobes "sg" of the Mecopteron shown in Fig. 21. The structure labeled "ep" in Fig. 20 probably represents the tenth tergite, or the fusion product of the tenth tergite and the paraprocts (or plates on either side of the anus). I formerly interpreted the structures labeled "s" in Fig. 20, as the penis valves (*i. e.* "pv" of other insects, Figs. 17, 21, etc.); but there are some grounds for considering the structures "s" of Fig. 20, as the remains of the gonopods labeled "s" (which are composed of the segments "g" and "h" in other insects), or a portion of it, in the other figures, and I have provisionally adopted the latter interpretation in the present paper.

In the psyllid shown in Fig. 14, the tergal sclerites labeled 6

and 7, probably represent the eighth tergite, and the structure labeled "ep" bears the anus at its tip (*i. e.* it is a "proctiger"). The proctiger "ep" probably represents the tenth tergite united with the ninth, although the embryology of these insects would have to be studied in order to definitely determine what segments enter into the composition of the structures in question. The structure labeled "g" is here interpreted as representing the united basal segments of the gonopods (labeled "g" in other figures—as in Fig. 21 for example) though it may also include the ventral plate "ha" of other insects as well. The forceps "h" of Fig. 14 apparently represent the distal segments of the gonopods "h" of other figures. All that remains of the phallus or ædeagus, is the slender bowed structure "pv," which bears a terminal articulated appendage or "telædeagus" fitting into the groove on the lower (posterior) surface of the proctiger "ep." In the fulgorid shown in Fig. 16, the structure bearing the label "8?" probably contains the ninth segment; but it appears to be the eighth. The dorsal structure labeled "ep" is apparently formed in great part by the ninth tergite which has probably united with the tenth tergite, and has grown downward and posteriorly below the anal opening. The structure "ep" is thus a "proctiger" rather than an "epiproct," though either term might be applied to it. The forceps "s" of Fig. 16 represent either the styli (gonopods) of other figures (labeled "s") or they represent portions of these styli (gonopods); and the inner structures "pv" which they enclose, are probably homologous with the penis valves "pv" of other insects. It is quite possible that the structure "ep" of Fig. 16 may represent a union of the structures labeled "sg" and "ep" in Fig. 20; but I have been unable to determine this point.

The tergal region "ep" of the Trichopteron shown in Fig. 15 probably represents the ninth, or the united ninth and tenth tergites, while the lateral lobes "sg," are apparently homologous with the copulatory lobes "sg" of Figs. 20 and 21. The structure labeled "pv" in Fig. 15 is the ædeagus or phallus, and is possibly composed of the united penis valves of certain other forms. The gonopods "s" of Fig. 15 are two-segmented (*i. e.* are made up of segments "g" and "h") and are apparently homologous or homodynamous with the styli "s" (also composed of two segments

"g" and "h") of the trichopterous larva shown in Fig. 6(Plate III). The basal plate "p" of Fig. 6 (Plate III) has been provisionally homologized with the styli-bearing plate "p" of Fig. 11 (Plate IV) but this may prove to be incorrect. While it is quite probable that the gonopods "s" of the adult Trichopteron shown in Fig. 15 (Plate IV) are homodynamous, or serially homologous, with the gonopods labeled "s" in Fig. 6 (Plate III) of a larval Trichopteron, in the sense that the legs of the mesothorax are serially homologous (homodynamous) with those of the metathorax, the two structures in question may not be *absolutely* homologous, since the gonopods or styli labeled "s" in the larval Trichopteron (Fig. 6, Plate III) are apparently borne on the *tenth* segment, as is also true of the styli in certain larval sawflies, while the gonopods of the adults may not belong to the tenth segment. The question naturally arises as to whether the styli borne on the tenth segment of the larval Trichopteron ("s" of Fig. 6, Plate III) form the gonopods "s" of the adult (Fig. 15, Plate III) or whether they represent the penis valves which unite to form the phallus of the adult. The observations of Wheeler, 1893, who maintains that the penis valves are appendages of the tenth segment, would lend weight to the latter view; but it is much simpler to refer to both styli "s" of larvæ (Fig. 6, Plate III) and gonopods "s" of adult insects (Fig. 15, Plate IV) as gonopods or gonostyles regardless of the segment to which they belong; and for the sake of convenience, this method has been adopted in the present discussion.

The dorsal region "ep" of the Lepidopteron shown in Fig. 13, represents either a posterior prolongation of the ninth tergite, or the fusion product of the tenth tergite with the ninth. The lateral lobes "sg" are probably homologous with the copulatory lobes "sg" of Fig. 21, or the lateral lobes "sg" of the Trichopteron shown in Fig. 15. The structure labeled "pv" in the Lepidopteron (Fig. 13) is the phallus or ædeagus, and the filament "b" possibly represents the coiled filament "b" of Fig. 21. The harpago "h" of the Lepidopteron is possibly the terminal segment of the gonopod, whose basal portion has united with the ninth abdominal segment; or the harpago "h" may represent the whole gonopod "s" of Fig. 15, although the former explanation is the more probable one. The dorsal structure "ep" of the Lepidopteron (Fig. 13) is some-

times called the uncus or tegumen, and a ventral prolongation possibly homologous with the lower portion of the structure labeled "ep" in Fig. 16 is sometimes called the scaphium in Lepidoptera.

In the Dipteron shown in Fig. 10, the dorsal plate "ep" is probably the tergite of the ninth segment alone; but I am not sure of this point. The elongate slender processes "sg" resemble cerci; but I am more inclined to regard them as lateral processes of the ninth tergite possibly homologous with the lateral lobes "sg" of Fig. 21, and I have therefore referred to them as the surgonopods in the following discussion. They are possibly homologous with the structures referred to as "gonopods" in such Neuroptera as *Ithone* (See Crampton, 1918a Fig. 14); but these structures in both cases are probably homologous with the parts termed surgonopods in the insects described in the present paper. I would likewise use this opportunity of calling attention to the fact that the lateral plates called paraprocts in the paper referred to above as dealing with the Neuroptera, etc. (Crampton, 1918a) are not the true paraprocts "pr" of Figs. 11, 12, etc., but are homologous with the lateral plates of the ninth segment called gonopleurites in the present paper ("pp" of Figs. 20, etc.). The basal segment of the gonopods labeled "g" in Fig. 10 has probably united with the pleural region to form the apparent basal segment "g," while the distal segment "h" is distinct and well developed. The terminal portions of both gonopods "h" and surgonopods "sg" bear short spine-like structures which are apparently of use in enabling the forceps-like structures to hold more securely. The sternite of the ninth abdominal segment "ha," forms a hypandrium or plate below the genitalia of the male, as in the Neuroptera and sawflies.

The principal points brought out in the preceding discussion may be briefly summarized as follows. The epiproct, or plate above the anal opening ("ep" of Figs. 11, 17, etc.) is usually formed by the tenth tergite, or the tenth united with the ninth tergite (or a portion of it). In some cases the region above the anal opening may grow downward on either side, or unite with other regions to form a proctiger ("ep" of Fig. 16?) through which the alimentary tract opens. Lateral prolongations of the ninth tergite form the surgonopods "sg," or dorsal structures frequently employed as upper claspers in mating. The pleural plates of the

ninth abdominal segment form the gonopleurites "pp," while the sternite of the ninth segment usually forms the hypandrium "ha" or plate below the genitalia of the male. When the cerci "ca" are present, they are borne on a region representing the union of the paraprocts of the eleventh segment ("pr" of Fig. 12) fused with the tenth tergite, as in Fig. 17, and this in turn may unite with the ninth tergite. In the lower insects a pair of styli "s" or gonopods is attached to the posterior margin of the hypandrium (ninth sternite), or plate below the genitalia of the male. In higher insects a pair of styli (gonostyli, or gonopods) forms the outer ventral pair of claspers "s" between which the penis valves "pv" or phallus are situated. The only structures which one can compare with these gonostyli or gonopods in larval insects, are borne on the tenth sternite (Fig. 6, "s") as in larvæ of Trichoptera, certain sawflies, etc.

From a study of the wing veins, and head region, I formerly maintained that the Homoptera (and Hemiptera) are somewhat more closely related to the insects grouped about the Psocidæ than to those grouped about the Neuroptera. The thoracic sclerites of the Homoptera, however, are very like those of the Neuroptera, and the genitalia of the male Fulgoriadæ, Psyllidæ, etc., here studied would bear out the view that the Homoptera are more closely allied to the Neuroptera and other Neuropteroid insects such as the Mecoptera, Lepidoptera, etc. The nature of the genitalia of the Strepsiptera would tend to confirm the contention that these insects are quite closely related to the Homoptera, such as the Psyllidæ, etc., although they show considerable resemblance to the Mecoptera and other Neuropteroid insects. The genitalia of the Diptera are like those of the Mecoptera and Trichoptera, and the lower Trichoptera are very similar to the lower Lepidoptera, as one would expect from a study of other features than the genitalia. The genitalia of the sawflies are as much like those of the Mecoptera as any insects, although they exhibit some resemblances to the genitalia of the Diptera also. In the main, the study of the genitalia of the higher insects would serve to substantiate the evidences of relationships furnished by other anatomical structures, and it would therefore be in harmony with the views concerning the interrelationships of the insects related to the Neuroptera, recently published in the Transactions of the Entomological Society of London (Crampton, 1919a).